

OBSERVATIONS ON THE REPRODUCTIVE BIOLOGY OF THE ANGULAR ROUGH SHARK, *OXYNOTUS CENTRINA* (OXYNOTIDAE)

by

Christian CAPAPÉ (1), Amadou A. SECK (2) & Jean-Pierre QUIGNARD (1)

ABSTRACT. - Some aspects of the reproductive biology of the angular rough shark are described in this paper from specimens collected in the Mediterranean (Tunisian coasts and Gulf of Lion, Southern France) and in the Eastern Tropical Atlantic (Cape Verde Peninsula, Senegal). At sexual maturity, males and females have attained a total length (TL) of 600 and 650 mm, respectively. Adult females were generally larger than males. The maximum TL for males and for females was 640 and 780 mm, respectively. The smallest gravid female observed was 730 mm TL. The angular rough shark is an aplacental viviparous species with two ovaries and two uteri, both of which are functional. Ripe oocytes ready to be ovulated were large and heavy. Their average diameter was 39.31 mm and their average weight was 24.45 g. Vitellogenesis of maturing oocytes did not coincide with gestation. Reproductive cycle could last approximately one year. Average weight and average TL of full developed fetuses were 69.65 g and 221.33 mm. Average weight and average TL of new born pups were 69.83 g and 228.33 mm TL. Birth probably occurred at a TL between 210 and 240 mm. The computed chemical balance of development (CBD) based on mean dry weights of new-borns pups and fertilised eggs was 1.36. The low CBD value was due to the fact that the angular rough shark was strictly a lecithotrophic species. Increase in weight especially among adults was more rapid in females which were generally heavier than males. This characteristic was related to the reproductive activities of the females. The liver is heavy and the hepatosomatic index (HSI) reached high values in all specimens. HSI is not subject to change with size except in females where it increased at the end of maturation and slightly decreased from July to September. Liver plays an important role in buoyancy rather than in elaboration of gonadic products. The gonosomatic index (GSI) reached high values in adults especially in females from July to September. The sex ratio of the total sample showed that males were slightly more numerous than females. The changes in sex ratio are related to sampling as well as to segregation of the sexes at different depths during certain stages of the reproductive cycle rather than to a high rate of mortality in juveniles and adults according to the sex.

RÉSUMÉ. - Observations sur la biologie de la reproduction de la centrine, *Oxynotus centrina* (Oxynotidae).

Certains aspects de la biologie de la reproduction de la centrine sont décrits dans cette note à partir de spécimens récoltés en Méditerranée (côtes tunisiennes et golfe du Lion au sud de la France) et dans l'Atlantique oriental tropical (presqu'île du cap Vert au Sénégal). La taille à la première maturité sexuelle est atteinte par les mâles et les femelles dès 600 et 660 mm de longueur totale (LT), respectivement. Chez les adultes, les femelles sont plus grandes que les mâles, les LT maximales étant respectivement de 780 et 640 mm. La plus petite femelle gravide observée mesurait 730 mm LT. La centrine est vivipare aplacentaire et possède deux ovaires et deux utérus, tous fonctionnels. Les ovocytes matures, prêts à être pondus, sont volumineux et lourds. En moyenne, leur diamètre est de 39,31 mm et leur masse de 24,45 g. Le cycle de reproduction dure probablement un an et l'activité vitellogénétique n'est pas concomitante de la gestation. En moyenne, les nouveau-nés mesuraient 228,33 mm LT et leur

(1) Laboratoire d'Ichtyologie, case 102, Université des Sciences et Techniques du Languedoc Montpellier II, 34095 Montpellier, cedex 5, FRANCE. [capape@univ-montp2.fr]

(2) Institut fondamental d'Afrique noire Cheikh Anta Diop, Musée de la Mer, Gorée, SÉNÉGAL.

pas concomitante de la gestation. En moyenne, les nouveau-nés mesuraient 228,33 mm LT et leur masse était de 69,83 g. La taille à la naissance se situait probablement entre 210 et 240 mm LT. La balance chimique de développement (BCD), fondée sur les masses moyennes sèches des nouveau-nés et des œufs fécondés, est de 1,36. Cette faible valeur est due au fait que la centrine est une espèce strictement lécithotrophe. La croissance pondérale semble plus rapide chez les femelles et celles-ci étaient généralement plus lourdes que les mâles, surtout chez les adultes en raison des activités de reproduction des femelles. La masse du foie est élevée et le rapport hépatosomatique (HSI) atteint des valeurs importantes chez tous les individus. Le HSI ne varie pas avec la taille sauf pour les femelles chez lesquelles il s'accroît à la fin de la maturation et décroît légèrement de juillet à septembre. Le foie semble jouer un rôle plus important dans la flottabilité que dans l'élaboration des produits gonadiques. Le rapport gonosomatique atteint des valeurs élevées chez les femelles adultes et en particulier pendant la période de reproduction. La sex-ratio de l'échantillon montre que les mâles sont légèrement plus nombreux que les femelles. Les variations de la sex-ratio en fonction de l'état des individus peut s'expliquer par des biais d'échantillonnage et par la ségrégation des sexes en fonction de la profondeur plus que par une plus grande mortalité d'une catégorie d'individus.

Key-words. - Oxynotidae, *Oxynotus centrina*, MED, Tunisian coasts, Gulf of Lion, Senegal, Mediterranean, ASE, Eastern Tropical Atlantic, Distribution, Reproductive biology.

Oxynotids are generally considered uncommon in their fishing areas. Among them, the angular rough shark, *Oxynotus centrina*, has been recorded from the Eastern Atlantic and the Mediterranean. Little is known about its reproductive biology. Some information was previously summarised by Moreau (1881), Poll (1951), Tortonesi (1956), Bini (1967), Cadenat and Blache (1981), Compagno (1984), Quérou (1984) and Springer (1990).

The study of angular rough sharks from three marine localities allow us to expand on the previous data. This paper gives details on size at sexual maturity, size at birth, reproduction, fecundity and sex-ratio of this species.

MATERIAL AND METHODS

A total of 99 free living specimens and 12 fetuses were observed. The monthly distribution of the captures of *O. centrina* is summarised in table I. The geographic and bathymetric distributions of their capture sites are presented in table II. Thirty-two specimens were collected by demersal trawls off the northern coasts of Tunisia (Central Mediterranean) from 1970 to 1985. Angular rough sharks from the Gulf of Lion (Southern France, Northern Mediterranean) were caught off the Palavasian shore from 1988 to 1993: 48 specimens by gill-nets and 16 by demersal trawls.

Three specimens were caught by gill-nets from off the Cape Verde Peninsula (Senegal, Eastern Tropical Atlantic) from 1993 to 1998.

Because no morphological, biometrical, and biological intraspecific variations were observed among the specimens from these three marine areas, they were combined in one sample.

Measurements to the nearest millimetre were made according to Collenot (1969). They included total length (TL), clasper-length (CL) from the forward rim of pelvic girdle to the tip of claspers.

Body and liver were weighed to the nearest gram, whilst testis and ovaries to the nearest centigram. Ripe oocytes ready to be ovulated were removed from the ovaries. Fertilised eggs and full developed foetuses were removed from the uteri. They were then counted, measured and weighed to the nearest centigram.

In full developed foetuses, the umbilical stalk and yolk sac were totally reabsorbed and a scar marked the site of the umbilical stalk. These foetuses possessed an internal vitellin vesicle.

To determine the onset of sexual maturity in males, the CL to TL and the testis weight (GW) to TL relationships were used. According to Bass *et al.* (1975) and to Stevens and Lyle (1989), the claspers of juveniles are short and flexible, and grow in relation to shark TL. In adult males, the claspers were elongated, larger than the pelvic fin, rigid and their cartilages were calcified. In females, two classes of specimens were distinguished by the condition of the ovaries and the morphology of their reproductive tracts. Juveniles had oocytes of microscopic size and membranous oviducts. Their nidamental glands were inconspicuous. Adults possessed two functional ovaries with yellow yolked oocytes from

Table I. - Monthly distribution by size and sex of *Oxynotus centrina*.

Month	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Total
Categories													
Newborn males	-	-	-	4	-	-	1	-	1	-	-	-	6
Juvenile males	2	3	6	-	1	4	8	6	-	2	-	-	32
Adult males	-	-	4	-	-	-	2	5	1	-	-	-	12
Total	2	3	10	4	1	4	11	11	2	2	-	-	50
Newborn females	-	-	-	-	-	-	-	-	2	-	-	-	2
Juvenile females	5	1	2	2	4	2	3	6	-	3	-	-	28
Adult females	-	-	-	1	-	-	4	6	3	1	-	-	15
Gravid females	-	-	-	-	-	-	-	4	-	-	-	-	4
Total	5	1	-	3	4	2	7	16	5	4	-	-	49
Grand total	7	4	12	7	5	6	18	27	7	6	-	-	99

Table II. - Geographic and bathymetric distribution of three populations of *Oxynotus centrina*. T: Tunisia. Males and females were separately studied; GL: Gulf of Lion; S: Senegal.

Depths	60-100 m			100-200 m			> 200			Grand total
Area	T	GL	S	T	GL	S	T	GL	S	
New-born males	-	6	-	-	-	-	-	-	-	6
Juvenile males	-	15	-	13	-	-	4	-	-	32
Adult males	-	6	-	1	-	-	-	5	-	12
Total	-	27	-	14	-	-	4	5	-	50
Total	27			14			9			50
New-born females	-	-	2	-	-	-	-	-	-	2
Juvenile females	-	10	-	-	6	-	12	-	-	28
Adult females	-	8	-	2	5	-	-	-	-	15
Gravid females	-	3	1	-	-	-	-	-	-	4
Total	-	21	3	2	11	-	12	-	-	49
Total	24			13			12			49
Grand Total	51			27			21			99

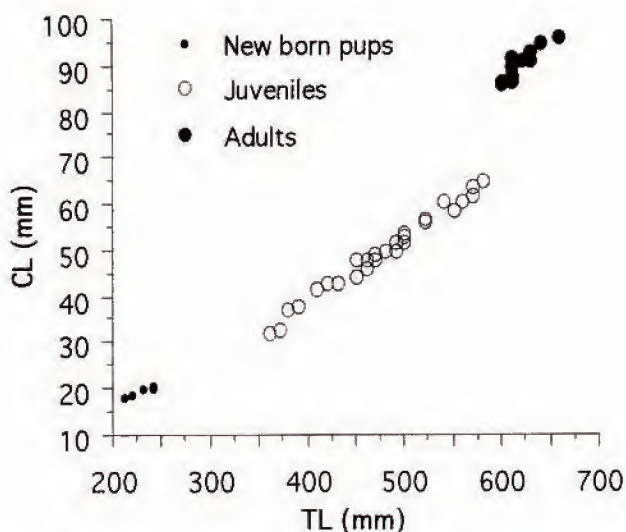


Fig. 1. - Clasper-length (CL) versus total length (TL) relationship in male *Oxynotus centrina*.

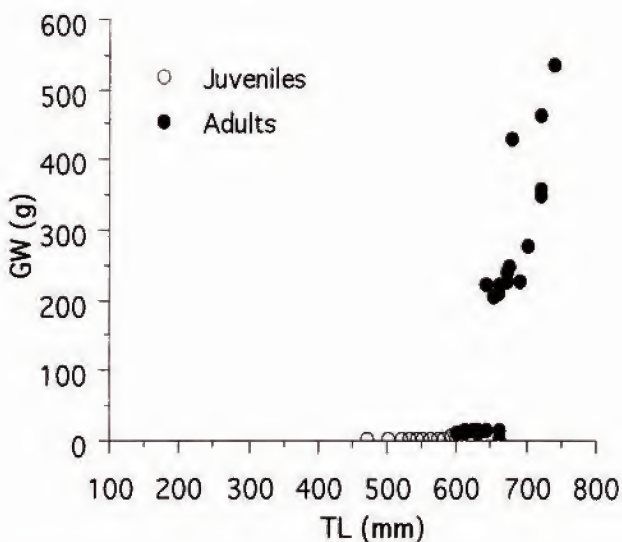


Fig. 2. - Testes-weight (GW) versus total length relationship (TL) in male *Oxynotus centrina*.

28 to 41 mm in diameter. The two uteri were fully developed and functional. Nidamental glands were conspicuous, and slightly rounded.

Among the juveniles, new born pups were considered separately. They exhibited a more or less reabsorbed internal vitelline vesicle and a unhealed scar. Their TL, however, were closely related to those of the full developed foetuses.

mean dry weights of fertilised eggs and fully developed foetuses. CBD is the mean dry weight of fully developed foetuses divided by the mean dry weight of fertilised eggs. Based on chemical analyses of the lesser spotted dogfish, *Scyliorhinus canicula*, water content of 50% in fertilised eggs and 75% in recently pupped individuals can be taken as standard values (Mellinger and Wise, 1989). CBD is a tentative estimate.

To study the growth in weight, the total body weight to TL relationship was used. Two biological indices were also calculated: the hepatosomatic index (HSI) and the gonosomatic index (GSI). The former was defined as $HSI = 100 \text{ LW/EW}$ and the latter as $GSI = 100 \text{ GW/EW}$, where EW is the eviscerated body weight of fish, LW and GW, the liver and the gonad weights respectively.

Tests for significance ($p < 0.05$) were performed by using analysis of variance and the Student *t*-test. Correlations were assessed by least-squares regression. Comparisons of curves were made by ANCOVA.

RESULTS

Distribution and habitat

Although captures of angular rough sharks occurred from January to October, they were relatively more frequent in March, July and August (Table I). Adult females were only found from April to October, among which four gravid specimens were caught in August.

Specimens of *O. centrina* from the Gulf of Lion were relatively the most numerous. They were generally caught between 60 and 100 m depth. Juveniles were more numerous than adults both in the total sample and for each of the three areas. All the specimens of *O. centrina* were caught on sandy, muddy and sandy-muddy bottoms.

Size at sexual maturity

Males. - The CL to TL and TW to TL relationships are plotted in figures 1 and 2, respectively. They show a point of inflexion, due to two growth phases. The first phase included 32 juveniles between 210 and 590 mm, whilst the second 12 adults between 600 and 660 mm. Among the juveniles, 6 new-born pups from 210 to 240 mm might be considered separately.

Females. - Two new-born pups, 26 juveniles and 19 adults were distinguished. The new-born pups were 220 and 240 mm, and the juveniles between 360 and 610 mm. The smallest adult female was 640 mm. Among the adults, 15 were non-gravid with developing or ripe oocytes. Four were gravid: 3 of which had fertilised ova and a single specimen bore full developed foetuses. All the gravid females exhibited degenerating oocytes in their ovaries. The smallest gravid female was 730 mm.

Size at birth

The length of full developed foetuses ranged from 215 to 235 mm (mean: 221.33 mm; s.e.: 9.96), and their weight from 66.2 to 75.5 g (mean: 69.65 g; s.e.: 2.67). The length of new-born pups ranged from 210 to 240 mm (mean: 225.00 mm; s.e.: 11.95) and their weight from 66 to 73 g (mean: 70.12 g; s.e.: 2.10).

Reproduction

The angular rough shark is an aplacental viviparous species. It has two ovaries and two uteri, both of which are functional. The ovaries produced cohorts of oocytes similar in size and in weight. One of these cohorts developed ripe oocytes, the others became atretic and degenerated. The diameter of ripe oocytes, ready to be ovulated, ranged from 38 to 41 mm (mean: 39.31 mm; s.e.: 1.11) (Table III). Ten adult females exhibited a phase of active vitellogenesis with growing or ripe oocytes in their ovaries, whilst their uteri were in a resting phase. In contrast, the ovaries of gravid females were in a quiescent phase. The fertilised eggs were not encapsulated. Three new-born pups were caught at the beginning of April and three more at the end of July. The gravid female with full developed foetuses was caught in August.

Chemical balance of development

The average weights of ripe oocytes (mean: 24.45 g; s.e.: 1.60) and fertilised eggs (25.61 g; s.e.: 1.21) were closely related. This is also the case for the average weight of full developed foetuses (mean: 69.65 g; s.e.: 2.67) and new-born pups (mean: 70.12 g; s.e.: 2.10). The computed CBD for *O. centrina* is 1.36.

Weight-growth relationships

The relationships EW vs TL for both sexes did not show significant difference ($p < 0.05$) in slopes between sexes:

males: $\text{Ln EW} = 3.579 \text{ Ln TL} - 15.406$; females: $\text{Ln EW} = 3.579 \text{ Ln TL} - 15.291$

Table III. - Condition of ovaries and uteri in 19 adult female *Oxynotus centrina*.

Month of catch	Female size (TL, mm)	Ovarian activity	Oocytes diameter range (mm)	Uteri content
Apr	720	vitellogenesis	40 - 41	rest
Jul	670	vitellogenesis	38 - 39	rest
Jul	680	vitellogenesis	38 - 39	rest
Jul	690	vitellogenesis	28 - 30	rest
Jul	740	vitellogenesis	40 - 41	rest
Aug	720	vitellogenesis	40 - 41	rest
Aug	660	vitellogenesis	38 - 39	rest
Aug	660	vitellogenesis	38 - 39	rest
Aug	670	vitellogenesis	36 - 39	rest
Aug	700	vitellogenesis	38 - 39	rest
Aug	720	vitellogenesis	38 - 39	rest
Aug	730	rest	microscopic	eggs
Aug	780	rest	microscopic	eggs
Aug	780	rest	microscopic	eggs
Aug	745	rest	microscopic	foetuses
Sep	660	vitellogenesis	38 - 39	rest
Sep	640	vitellogenesis	31 - 32	rest
Sep	653	vitellogenesis	33 - 36	rest
Oct	675	vitellogenesis	38 - 39	rest

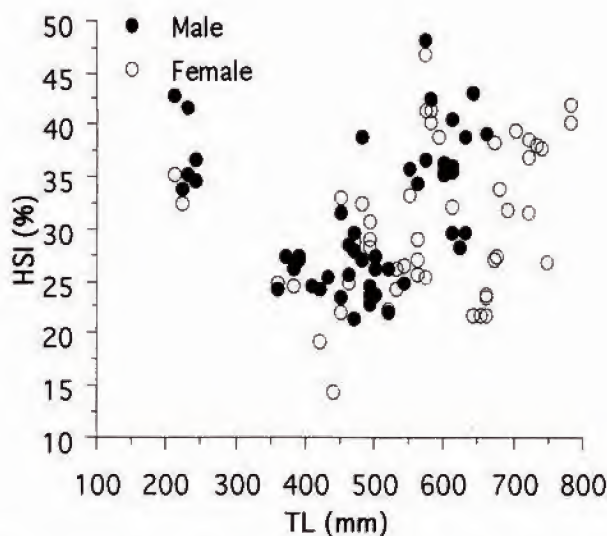


Fig. 3. - Values and variations of the hepatosomatic index (HSI) versus total length (TL) in male and female *Oxynotus centrina*.

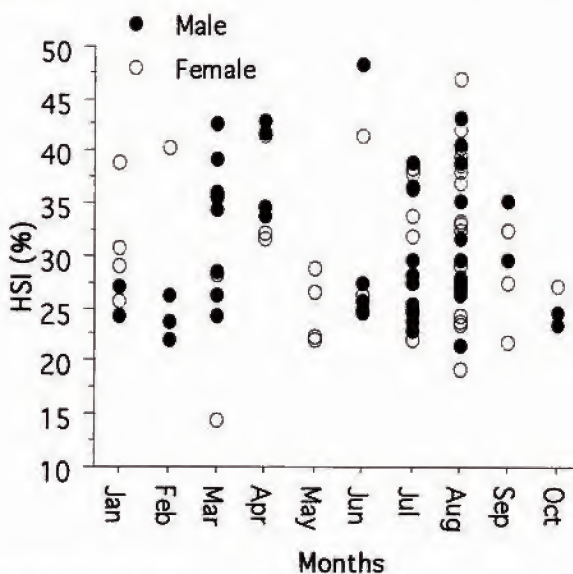


Fig. 4. - Values and variations of the hepatosomatic index (HSI) versus months in male and female *Oxynotus centrina*.

Biological indices

The relative liver weight increased with respect to total body length in specimens of both sexes. However, it increased more rapidly in females than in males (Fig. 3). HSI

had similar values in both males and females (Table IV). It changed according to the size and the category of specimens. It was significantly higher in new-born males and all adults than in juveniles. HSI did not show significant changes during the year, however it slightly decreased from July to September (Fig. 4).

GSI reached the highest value in the adults, among which it was higher in females than in males (Fig. 5). Among the former, it was relatively higher from July to September (Fig. 6).

Fecundity

Oocytes and ripe oocytes ready to be ovulated are statistically more numerous in the left ovary than in the right one. In contrast, fertilised eggs and full developed foetuses are equally distributed in both uteri. Ovarian fecundity (OF) based on the number of ripe oocytes ranged from 9 to 22 (mean: 14.50; s.e.: 4.42). Uterine fecundity (UF) ranged from 10 to 12 (mean: 10.66; s.e.: 1.15). OF is correlated with the size of the females: $OF = 0.132 TL - 76.426$; $r = 0.840$.

Sex-ratio

Full developed male and female foetuses were equally distributed in both uteri of the observed female (Table V). New-born male pups are more numerous than females. This was also true for juveniles and for the total sample. In contrast, adult females are more numerous than adult males.

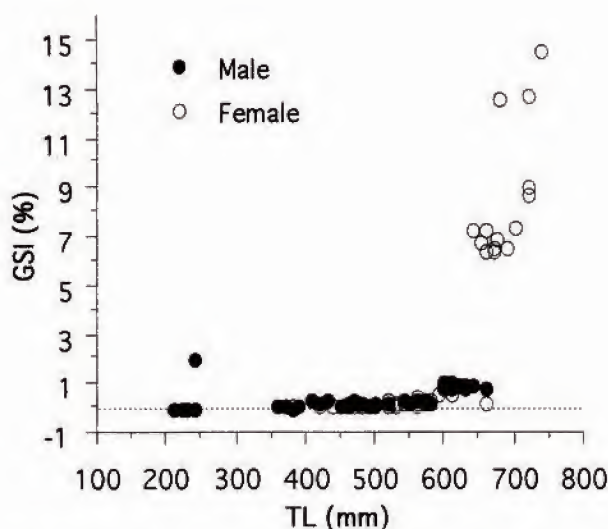
DISCUSSION

The Atlanto-Mediterranean abundance of *O. centrina* is subject to change according to the area. The species is less rare in the Mediterranean, especially in the Gulf of Lion, than in the Atlantic off the eastern coast of France. This aspect could be related to the fishing pressure.

The records of catches were relatively frequent between 60 and 100 m depth. They concerned all the new-born pups and practically all the adult males and females, including all the gravid females. These observations agree with Castro (1993). They suggest that the adult specimens approached the coast for mating and to give birth rather than segregating at different depths according to sex and sexual condition.

Table IV. - Values of HSI according to the different categories of male and female *Oxynotus centrina*.

Category	n	Range	Mean	s. e.
New-born males	6	34.69 - 42.85	37.59	3.80
Juvenile males	32	21.45 - 32.74	28.23	5.80
Adult males	12	29.65 - 43.25	35.79	4.61
Total males	50	21.45 - 43.25	33.87	4.96
New-born females	2	32.65 - 35.41	34.03	1.95
Juvenile females	28	19.28 - 46.79	28.68	7.09
Adult females	19	23.48 - 42.21	34.32	5.86
Total females	49	19.28 - 46.79	32.34	3.17
Grand total	99	19.28 - 46.79	33.10	3.82



O. centrina. Therefore, the extreme paucity of the two species in these areas probably reduces to a minimum a paucity competition between them.

During sexual maturation the claspers grew rapidly as males attained a size at first sexual maturity of 610 mm TL for Mediterranean specimens. Females began sexual maturation at 560 mm TL and they were fully mature at 660 mm. They probably mature later than males and this characteristic could explain why they reach a larger size. The largest male and female of *O. centrina* examined in this study were 640 and 730 mm respectively. However, Quignard *et al.* (1962) observed a specimen of 900 mm caught off Sète (southern France). Quéro (1984) wrote that *O. centrina* could reach 1500 mm. Among the larger specimens of the sample studied herein, males and females *O. centrina* had an average TL of 622.00 and 704.66 mm, respectively. A comparison test showed that these TL are significantly different. The difference in TL between male and female *O. centrina* is another instance of sexual size dimorphism among elasmobranchs and particularly among viviparous species. Similar observations have been reported by Mellinger (1989) who wrote that this phenomenon is probably linked to reproductive strategies in elasmobranchs.

Risso (1826) noted that off Nice this shark mated in February and the parturition occurred three months after. From specimens fished in the Bay of Naples, Lo Bianco (1909) observed eggs at the beginning of their segmentation in February, embryos of 30 mm TL in January (?), and more advanced embryos of 150 mm TL with large yolk sac in March. New-born pups were caught in April and in September. *O. centrina* clearly reproduced throughout the year in the Mediterranean. However, previous and recent observations are not sufficient to show exact breeding periodicity in *O. centrina*. They are statistically inadequate to delineate an annual reproductive cycle in *O. centrina*. In contrast, they could suggest that the gestation period might last several months or probably one year.

The large and heavy oocytes allow us to conclude that *O. centrina* is purely a lecithotrophic elasmobranch as defined by Wourms (1977, 1981). In this species, transfer of stored nutrients from yolk to embryo generally requires a long time (Wourms *et al.*, 1988). A gestation period of several months and most likely of approximately one year appears to be a reasonable hypothesis. Thus, the possibility of two litters per year can be excluded. Females *O. centrina* with growing or ripe oocytes had empty, not enlarged uteri and clearly were in a resting phase. This observation indicates that vitellogenesis continues after parturition. Unfortunately, gravid females with embryos at different stages of development were not observed, but Risso (1826) and Lo Bianco (1909) did not describe the ovary's condition during the gestation in *O. centrina*. The single gravid female with full developed foetuses in its uteri did not exhibit vitellogenetic activity. Thus it seems that vitellogenesis does not coincide with gestation in *O. centrina* as in numerous other viviparous elasmobranchs. This phenomenon can last until the end of gestation as in

Table V. - *Oxynotus centrina* sex ratio for each category of specimens and for the total sample.

Category	Number of males	Number of females	Ratio (M:F)
Foetuses	6	6	1:1
New-born pups	6	2	3:1
Juveniles	32	28	1.14:1
Adults	12	15	0.80:1
Total	50	49	1.02:1
Grand total	56	55	1.02:1

torpedinids (Chieffi, 1961; Mellinger, 1981) or in *Centroscymnus* (Yano and Tanaka, 1988).

The lack of an egg capsule is another similarity among these species. This is also the case for *O. centrina*. Moreau (1881) found 16 oocytes of 60 μ m diameter in the ovaries of a female caught from off Arcachon (Atlantic coast of France). He did not report the presence of an egg capsule. These oocytes were significantly larger than those observed in the Mediterranean. According to Tortonese (1956), Bridge (1904) provided an illustration of an embryo 246 μ m TL caught off British isles. The exact stage of this embryo is unclear; it was possibly close to birth. Its TL is slightly longer than the average size of new-born pups and full developed foetuses that we observed.

The calculated CBD (1.36) is a relatively low value, closely related to that of *Torpedo* (0.8; Ranzi, 1932) and a little higher than *Centrophorus granulosus* and two squatinids (0.5; Ranzi, 1932; Capapé *et al.*, 1990). These data confirm that *O. centrina* is purely a lecithotrophic elasmobranch. In these viviparous species, the contribution of maternally-derived organic molecules to embryonic growth is not very important.

Weight difference between females and males are most notable in the adults; the former are generally larger and heavier than the latter. This difference appears related to egg production and the breeding activities of females.

The percentage liver weight and the HSI of the angular rough sharks reach high values in all categories of specimens even if they can change according to size. Cadenat and Blache (1981) reported similar values from specimens caught in the tropical Atlantic. According to Bone and Roberts (1969) and to Baldrige (1970, 1972), the density of elasmobranchs can be related to their bathymetric habits. *O. centrina* lives on deep-sea bottoms. This ecological characteristic, its general morphology, and the shortness of the pectoral fin area require a significant static lift from its liver. Therefore, the liver of the angular rough shark probably plays an important role in buoyancy and explains the high values of the HSI. Moreover, the HSI quickly increased as the juveniles approached the time of maturation. Then, it decreased considerably in adults. These variations indicated that a portion of hepatic reserves could be used for gonadal products, especially in females at the breeding period. This type of transfer of nutriment from liver to ovaries has been described in oviparous species (Craik, 1978; Capapé, 1980) as well as in viviparous species (Rossouw, 1987; Capapé and Zaouali, 1993, 1995). In *O. centrina*, it is corroborated by the concomitant GSI increase in adults. However, these phenomena are less evident in the males than in females as shown by GSI values in both sexes.

Ovarian fecundity is a little higher than uterine fecundity probably because some oocytes were not ovulated and became atretic. Similar observations were described by Yano (1995) for *Centroscyllium fabricii* from off western Greenland.

The three females with fertilised eggs in their uteri also had degenerating oocytes in their ovaries. Nine to 12 individuals seems to be the most probable litter size. Compagno (1984), Quéro (1984) and Springer (1990) provide similar data. Risso (1826) reported 23 embryos in a female. Moreau (1881) wrote that a female from Arcachon had 16 non embryonated eggs in her uteri. *O. centrina* is not a prolific species as other elasmobranchs (Dodd, 1983; Mellinger, 1989). Moreover, *O. centrina* probably has a long reproductive cycle and the consequences in terms of fecundity are very important. The conclusion is that its recruitment most likely is poor.

The sex ratio of the entire sample indicated that males were slightly more numerous than females. This is not the case for juveniles and adults. The apparent changes of sex ratio are probably due to sampling as well as segregation of the sexes at different

depths during certain stages of the reproductive cycle rather than a high rate of mortality according to the sex in juveniles and adults. This phenomenon has been previously described in other elasmobranchs species by several authors (Olsen, 1954; Babel, 1967; Klimley, 1987; Stevens and Lyle, 1987; Capapé and Zaouali, 1994).

Acknowledgements. - The authors are grateful to the fishermen from the fishing sites of Bizerta and La Goulette (northern Tunisia); Sète, Palavas-les-Flots and Carnon (southern France); Ouakam (Cape Verde Peninsula, Senegal) who provide them with material and to three anonymous referees for their useful and helpful comments on the manuscript.

REFERENCES

- BABEL J.S., 1967. - Reproduction, life history and ecology of the round stingray, *Urolophus halleri*. *Calif. Dept. Fish Game Fish Bull.*, 137: 1-131.
- BALDRIDGE H.D., 1970. - Sinking factors and average densities of Florida sharks as function of liver buoyancy. *Copeia*, 1970(4): 744-754.
- BALDRIDGE H.D., 1972. - Accumulation and function of liver oil in Florida sharks. *Copeia*, 1972(2): 306-325.
- BASS A.J., D'AUBREY J.D. & N. KISTNASAMY, 1975. - Sharks of the east coast of southern Africa. III. The families Carcharhinidae (excluding *Mustelus* and *Carcharhinus*) and Sphyrnidae. *Oceanogr. Res. Inst. (Durban), Invest. Rep. (S. Afr. Ass. Mar. Biol. Res.)*, (38): 1-100.
- BINI G., 1967. - Leptocardi, Ciclostomi, Selaci. In: *Atlante dei Pesci delle Coste italiane*, pp. 1-206. Milano: Mondo sommerso.
- BONE Q. & B.L. ROBERTS, 1969. - The density of elasmobranchs. *J. Mar. Biol. Ass. U.K.*, 49: 913-937.
- CADENAT J. & J. BLACHE, 1981. - Requins de Méditerranée et d'Atlantique (plus particulièrement de la côte occidentale d'Afrique). *Faune trop.*, ORSTOM, 21: 1-330.
- CAPAPÉ C., 1980. - Contribution à la biologie des rajidae des côtes tunisiennes. XIX. *Raja polystigma* Regan, 1923. Relations taille-poids du corps, du foie et des gonades. Rapports hépato- et gonosomatique. Coefficients de condition. *Cah. Biol. mar.*, 21: 363-373.
- CAPAPÉ C., QUIGNARD J.P. & J. MELLINGER, 1990. - Reproduction and development of two angel sharks, *Squatina squatina* and *S. oculata* (Pisces: Squatinidae), off Tunisian coasts: semi delayed vitellogenesis, lack of egg-capsule and lecithotrophy. *J. Fish Biol.*, 37: 347-356.
- CAPAPÉ C. & J. ZAOUALI, 1993. - Nouvelles données sur la biologie de la reproduction de la pastenague marbrée, *Dasyatis marmorata* (Steindachner, 1892) (Pisces, Rajiformes, Dasyatidae) des côtes méridionales de la Tunisie (Méditerranée centrale). *Ichthyophysiol. Acta*, 16: 1-34.
- CAPAPÉ C. & J. ZAOUALI, 1994. - Distribution and reproductive biology of the blackchin guitarfish, *Rhinobatos cemiculus* (Pisces: Rhinobatidae) in Tunisian waters (Central Mediterranean). *Aust. J. Mar. Freshw. Res.*, 45: 551-561.
- CAPAPÉ C. & J. ZAOUALI, 1995. - Reproductive biology of the marbled stingray, *Dasyatis marmorata* (Steindachner, 1892) (Pisces: Dasyatidae) in the Tunisian waters. *J. Aquacult. Aquat. Sci.*, 7: 108-119.
- CASTRO J.I., 1993. - The shark nursery of Bulls Bay, South Carolina, with a review of the shark nurseries of the southeastern coast of the United States. *Env. Biol. Fish.*, 38: 37-48.
- CHIEFFI G., 1961. - La luteogenesi nei selaci ovovivipari. Ricerche istologiche e istochimiche in *Torpedo marmorata* e *Torpedo ocellata*. *Pubbl. Stn. zool. Napoli*, 32: 145-166.
- COLLENOT G., 1969. - Étude biométrique de la croissance relative des ptérygopodes chez la petite roussette *Scyliorhinus canicula* L. *Cah. Biol. mar.*, 10: 309-323.
- COMPAGNO L.V.J., 1984. - FAO species catalogue. Vol. 4. Sharks of the world. An annotated and illustrated catalogue of shark species known to date. Part 1: Hexanchiformes to Lamniformes. *FAO Fish. Synop.*, (125), 4(1): 1-249.

- CRAIK J.C.K., 1978. - An annual cycle of vitellogenesis in the elasmobranch *Scyliorhinus canicula*. *J. Mar. Biol. Ass. U.K.*, 58: 719-726.
- DODD J.M., 1983. - Reproduction in cartilaginous fishes (Chondrichthyes). In: *Fish Physiology* (Hoar W.S., Randall D.J. & E.M. Donaldson, eds), pp. 31-95. New York: Academic Press.
- KLIMLEY A.P., 1987. - The determinants of sexual segregation in the scalloped hammerhead shark, *Sphyrna lewini*. *Env. Biol. Fish.*, 18(1): 27-40.
- LO BIANCO S., 1909. - Notizie biologiche riguardanti specialmente il periodo di maturità sessuale degli animali del golfo di Napoli. *Mitt. zool. Stn Neapel*, 19: 513-761.
- MELLINGER J., 1981. - Biologie et physiologie du développement, de la croissance et de la reproduction des torpilles: un aperçu des recherches depuis 1965. *Arch. Inst. Pasteur Tunis*, 58: 441-463.
- MELLINGER J., 1989. - Reproduction et développement des Chondrichthyens. *Océanis*, 15: 283-303.
- MELLINGER J. & J. WRIZEZ, 1989. - Biologie et physiologie comparée de deux sélaciens ovipares, les roussettes *Scyliorhinus canicula* et *Scyliorhinus stellaris*. Évolution de la matière sèche, de l'eau et des ions (Cl⁻, Na⁺, K⁺) dans le vitellus de *S. canicula* au cours du développement. *Bull. Soc. Zool. Fr.*, 114: 51-62.
- MOREAU E., 1881. - Histoire naturelle des poissons de la France. Vol. 1, 478 p. Paris: Masson.
- OLSEN A.M., 1954. - The biology, migration and growth of the school shark, *Galeorhinus australis* in southeastern Australian waters. *Aust. J. Mar. Freshw. Res.*, 5: 353-404.
- POLL M., 1951. - Poissons. I. Généralités, II. Sélaciens et Chimères. Rés. scient. Expéd. océanogr. belg. Eaux côt. afr. Atlant. Sud (1948-49), 4(1-3B): 1-154.
- QUÉRO J.-C., 1984. - Oxynotidae. In: *Fishes of the North-Eastern Atlantic and the Mediterranean* (FNAM), Vol. 1 (Whitehead P.J.P., Bauchot M.-L., Hureau J.-C., Nielsen J. & E. Tortonese, eds), pp. 126-127. Paris: UNESCO.
- QUIGNARD J.-P., RAIBAUT A. & J.P. TRILLES, 1972. - Contribution à la faune ichthyologique sétoise. *Nat. monspel.*, 4: 61-85.
- RANZI S., 1932. - Le basi fisio-morfologiche dello sviluppo embrionale dei Selaci I. *Pubbl. Stn. zool. Napoli*, 12(2): 209-290.
- RISSO A., 1826. - Histoire naturelle des principales productions de l'Europe méridionale et particulièrement de celles des environs de Nice et des Alpes maritimes, Vol. III, 486 p. Paris, Strasbourg.
- ROSSOUW G.J., 1987. - Function of the liver and hepatic lipids of the lesser sand shark, *Rhinobatos annulatus* (Müller & Henle). *Comp. Biochem. Physiol.*, 86B: 785-790.
- SPRINGER S., 1990. - Oxynotidae. In: *Check-List of the Fishes of the Eastern Tropical Atlantic* (CLOFETA), Vol. 1 (Quéro J.-C., Hureau J.-C., Karrer C., Post A. & L. Saldanha, eds), pp. 20-21. Paris: UNESCO.
- STEVENS J.D. & J.M. LYLE, 1989. - Biology of three hammerhead sharks (*Eusphyra blochii*, *Sphyrna mokarran* and *S. lewini*) from northern Australia. *Aust. J. Mar. Freshw. Res.*, 40: 129-146.
- TORTONESE E., 1956. - Leptocardia, Cyclostomata, Selaci. In: *Fauna d'Italia*, 2: 1-334. Bologna: Calderini.
- WOURMS J.P., 1977. - Reproduction and development in chondrichthyan fishes. *Amer. Zool.*, 17: 379-410.
- WOURMS J.P., 1981. - Viviparity: The maternal-fetal relationship in fishes. *Amer. Zool.*, 21: 57-67.
- WOURMS J.P., GROOVE J.P. & J. LOMBARDI, 1988. - The maternal-embryonic relationship in viviparous fishes. In: *Fish Physiology*, Vol XI (Hoar W.S. & D.J. Randall, eds), pp. 1-134. London: Academic Press.
- YANO K., 1995. - Reproductive biology of the black dogfish, *Centroscyllium fabricii*, collected from waters off western Greenland. *J. Mar. Biol. Ass. U.K.*, 75: 285-310.
- YANO K. & S. TANAKA, 1988. - Size at maturity, reproductive cycle, fecundity, and depth segregation of the deep sea squaloid sharks *Centroscymnus owstoni* and *C. coelolepis*. *Nippon Suisan Gakkaishi*, 54: 167-174.

Reçu le 02.02.1999.

Accepté pour publication le 30.06.1999.